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The holotype of the Carboniferous marattialean fern *Lobatopteris miltoni* (Artis)

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Synopsis. Previously reported as lost, the holotype of *Lobatopteris miltoni* (Artis) Wagner is stored in the British Museum (Natural History). The illustration published with the protologue misrepresents the proportion of pinnatifid pinnules in the frond, which has had important consequences for establishing its taxonomic position. Provisionally retained in *Lobatopteris*, it may eventually have to be transferred to another form-genus for larger, more divided fronds producing trilete spores.

INTRODUCTION

Lobatopteris miltoni (Artis) Wagner (syn. *Pecopteris miltoni* auctt.) is one of the most widely reported ferns from the Middle and Upper Carboniferous palaeo-equatorial floras, with over 200 pre-1961 references to it listed in *Fossilium Catalogus*. The traditional approach was to assign to it almost any piece of fern frond with predominantly elongate, pinnatifid pinnules. Dalinval (1960) has provided a much tighter circumscription, however, and has shown that many of the previous records were misidentifications. His is the best available analysis of the species, but one important aspect remains to be fully documented – the holotype. The only published illustration of it is the engraving accompanying the protologue (Artis 1825: pl. 14) and this does not clarify many of the details necessary to confirm Dalinval's interpretation. It has been stated that the specimen is lost (e.g. Wagner 1971), but it is in fact in the collections of the Department of Palaeontology, British Museum (Natural History). Since there are a number of discrepancies in Artis' illustration, we are providing here a photographic record of the specimen (Pl.1), together with a brief description and discussion.

Provenance and current location of specimen

The specimen was collected from 'that part of El-se-car new colliery, situated near Milton Furnace' (Artis 1825). The present-day Elsecar Colliery (NGR SE 392003) lies 1 km east of Milton, and is approximately midway between Sheffield and Barnsley. Artis gave no stratigraphical details, but the specimen was probably found near the Barnsley Seam (middle Westphalian B).

The specimen is now stored in the Department of Palaeontology, British Museum (Natural History), register no. V.4290. The wash drawing made in 1824 by J. Curtis, on which Artis based his illustration, is bound in with the museum's copy of the 1838 reprint of Artis' work.

DESCRIPTION

The specimen shows a part of a tri-/quadripinnate structure 15 cm long by 17·5 cm wide. 13 cm of primary rachis is preserved, which is 2·2–2·7 cm wide, with fine longitudinal striations.

Two secondary racheis, 0·4–0·5 cm wide, are attached 6 cm apart on the right side of the primary rachis (no secondary racheis are preserved on the left side). They are attached to the primary rachis at 50°–60°, arch sharply near their point of attachment and then lie at *c.* 80° to the primary rachis for most of their length. The secondary pinnae are parallel-sided as far as they are preserved. The longest pinna fragment is 15 cm, but is evidently very incomplete.

Tertiary racheis are attached at 80°–90° to the secondary racheis at intervals of 1·4–2·1 cm. They are *c.* 0·1 cm wide. The tertiary pinnae are parallel-sided for most of their length, and have a blunt terminal.

Most lateral pinnules are broadly attached, linguaeform to subtriangular, and lie at 60°–90° to the rachis. They are 0·6–1·0 cm long and 0·2–0·3 cm wide. The midvein is *c.* 0·05 cm wide, often decurrent at the base, and extends for at least three-quarters of the pinnule length. The pinnules are fertile, which masks details of the lateral veins. In most cases, all that remains of the sorus is the pedicle. Occasionally, however, isolated oval sporangia, *c.* 0·1 cm long, are still preserved. No structural details of the sporangia could be observed.

In the basiscopic part of the tertiary pinnae, the pinnules are more elongate, up to 1·2 cm long and 0·4 cm wide, and become pinnatifid. The pinnule lobes are rounded and *c.* 0·15 cm wide.

The apical pinnules are subrhomboidal, with a round apex, and are fused to the adjacent lateral pinnules.

DISCUSSION

Artis (1825) gave only the briefest description of the specimen:

Plate 1 *Lobatopteris miltoni* (Artis) Wagner. Holotype (V.4290) photographed under cross-polarized light. Natural size.

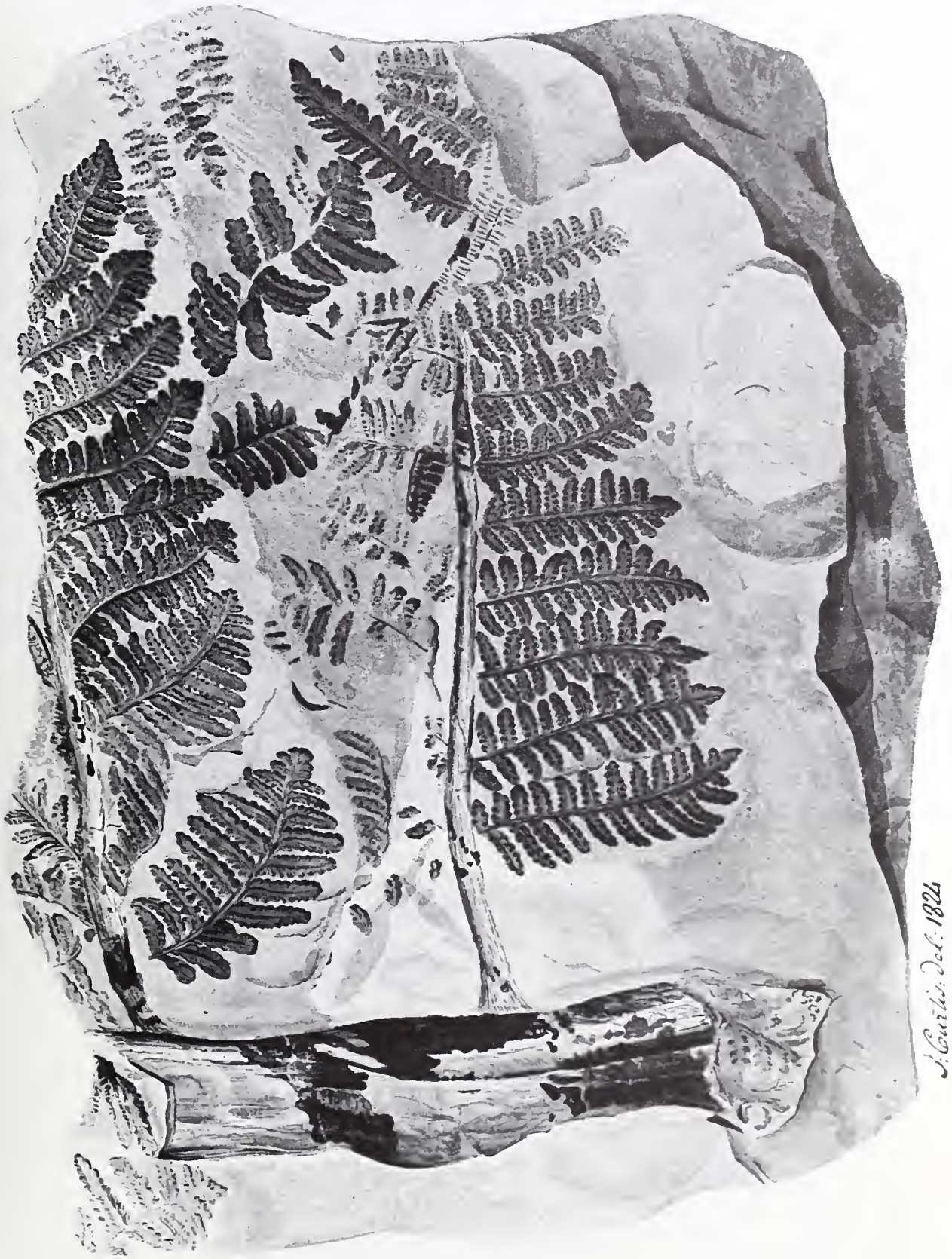
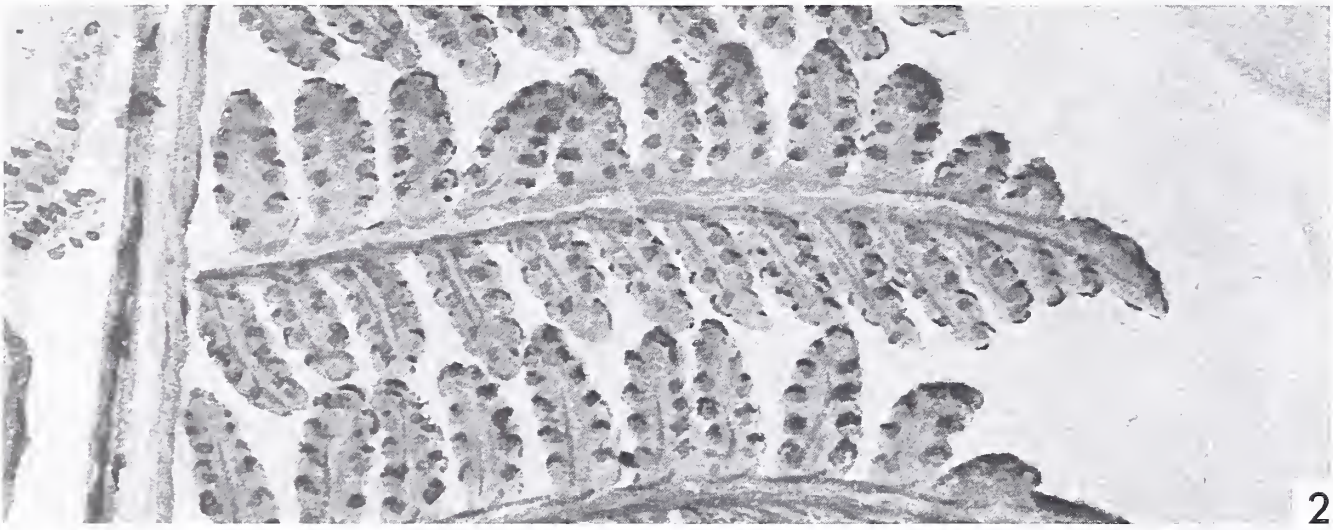


Plate 2 *Lobatopteris miltoni* (Artis) Wagner. Wash drawing of the holotype, made by J. Curtis, used as the basis for Artis' (1825: pl. 14) engraving. Natural size.



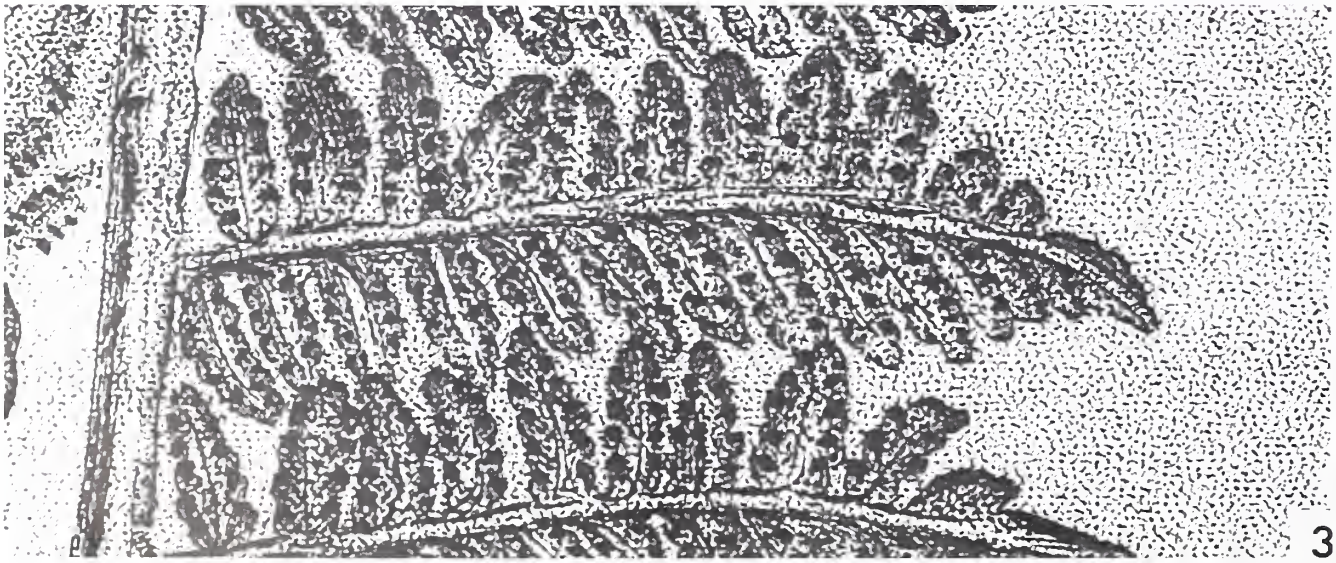


Plate 3 *Lobatopteris miltoni* (Artis) Wagner. Close-ups of part of holotype, all × 3. Fig. 1, photograph. Fig. 2, Curtis' wash. Fig. 3, Artis' engraving.

Frond tripinnate; stipes large, strong. Leaflets linear, tip rounded. Fructifications surrounding the leaflets near, but not entirely on, the margin.

He also admitted that the illustration was not entirely accurate. This inaccuracy probably arose during the engraving of the printing plate, since Curtis' original wash gives a somewhat better impression of the specimen (Pl. 2). In particular, the engraving grossly exaggerates the proportion of the pinnules that are pinnatifid; in fact only one ultimate pinna, near the base of the more distal secondary pinna, has well-developed pinnatifid pinnules. To illustrate this point, we have provided close-ups of part of the specimen as actually seen, as shown in Curtis' wash, and as represented in Artis' engraving (Pl. 3, figs 1–3). The error seems to have been because the specimen was fertile. Although few sporangia are preserved, there is a remnant disc of carbon where each sorus was originally attached to the pinnule, and this has imparted a superficially undulate appearance to the pinnule margin. The inaccuracy of the protologue illustration has had important implications in the interpretation of the species, which was widely believed (until Dalinval's 1960 revision) to be characterized by predominantly pinnatifid pinnules (e.g. Kidston 1924).

The holotype compares well with Dalinval's material in having blunt tertiary pinna terminals, and linguaeform to subtriangular lateral pinnules with a prominent, decurrent midvein. In particular, it is very similar to the large specimen in Dalinval's pl. 32, fig. 1. The primary rachis of the holotype is about twice as wide as in Dalinval's specimen and probably comes from a more proximal position in the frond. This may explain the smaller pinnules and more slender secondary racheis in Dalinval's specimen.

Because the holotype is fertile, it has not been possible to determine details of the lateral veins or whether there are epidermal hairs, which Dalinval regarded as important for distinguishing *L. miltoni* (Artis) from *Pecopteris bourozii* Dalinval and *P. lobulata* Dalinval. However, the holotype of *L. miltoni* (Artis) has much blunter pinna terminals and a more decurrent midvein than the other two species.

As already stated, although the holotype is fertile, only a very few, isolated sporangia are preserved. It is not possible, therefore, to determine the organization of the sori from this specimen. Wagner (1971) argued that Artis' engraving showed small fructifications near the margin of the pinnules, but these structures are in fact only the pedicles of the sori together with small, remnant discs of pinnule lamina which underlay the fructifications. However, a rather better preserved specimen of *L. miltoni* (Artis) figured by Dalinval (1960: pl. 40, fig. 2) shows closely spaced sori, comprised of four sporangia *c.* 0·05 cm in diameter. They correspond with the fructifications identified as *Cyathocarpus* Weiss (= *Asterotheca* auctt., *non* Presl) by Mosbrugger (1983), who established the combination *Cyathocarpus miltoni* (Artis).

Wagner (1959) has proposed that species with such fructifications could be further subdivided on characters of the sterile foliage. Using this principle, he established the form-genus *Lobatopteris*, for species with a high proportion of pinnatifid pinnules and a distinctive veining pattern (see also Cleal 1984: fig. 11). This pattern was described by Wagner (1959) as follows.

. . . the nervation . . . in its most simple form consists of only once bifurcate nervules, of which the upper branch dichotomizes mostly as well, so as to provide a characteristically threefold nervation. Afterwards, the middle branch of each nervuary group dichotomizes, which example is then followed by the lower and upper branches . . .

Wagner's diagnosis only mentions characters of the sterile foliage. However, he states in a preamble to the diagnosis that it belongs to the subfamily Miltonoidaea (family Caulopteridaceae), which Corsin (1955) defined on a number of characters, including the presence of *Asterotheca* auctt., *non* Presl sporangial clusters and the attachment of the fronds to *Caulopteris*-type stems. Consequently, *Lobatopteris* is not merely a generalized form-genus for a particular type of sterile foliage, but has a circumscription limited also by features of the fructifications and stem. Species such as *Pecopteris volkmannii* Sauveur, with lobatopteroid-like sterile foliage but different fructifications (in this case, of the *Senftenbergia*-type – Dalinval 1960), should be excluded from *Lobatopteris*.

Such a classification based on sterile characters might be regarded as suspect, and was not adopted by Mosbrugger. However, the species included in *Lobatopteris* by Wagner (such as *L. vestita* (Lesquereux), *L. micromiltoni* (Corsin) and *L. lamuriana* (Heer)) do appear to be significantly distinct from cyathocarpids with fewer pinnatifid pinnules and a simpler nervation (including *Cyathocarpus arborescens* (Brongniart), *C. cyatheus* (Brongniart) and *C. hemitelioides* (Brongniart)), and the generic distinction is probably justified.

Lobatopteris typically occurs in upper Westphalian D to Stephanian floras, but Wagner (1959) also included *L. miltoni* (Artis), which ranges from the Westphalian A to lower Westphalian D (Dalinval 1960). The branching of the lateral veins necessary to confirm this assignment cannot be seen in the holotype, but the sterile specimen figured by Dalinval (1960: pl. 32, fig. 1b) appears to show the diagnostic nervation pattern.

Unlike the more typical lobatopterids, *L. miltoni* (Artis) fronds have a much lower proportion of pinnatifid pinnules. This may simply be because these fronds are larger and more divided, the tertiary pinnae being equivalent to the pinnatifid pinnules of the more typical lobatopterids. There may be an analogy here with the medullosan pteridosperms, whose fronds were smaller and less divided in the Stephanian than in the Westphalian, probably in response to changing climatic conditions (Laveine 1967). Another possible difficulty is that Laveine (1970) has reported that *L. miltoni* (Artis) produced trilete spores (our attempt to prepare spores from the holotype was unsuccessful), in apparent contrast to the monolete spores produced by the more typical lobatopterids, such as *L. lamuriana* (Heer) and *L. micromiltoni* (Corsin). Here, again, the distinction may not be significant, however, since it is well documented that marattialean ferns can produce both trilete and monolete spores, sometimes even in the same plant (Hill & Camus 1986).

The generic position of *L. miltoni* (Artis) cannot be finally ascertained without more work on its morphological variation and fructifications. We have provisionally followed Wagner (1959) and retained it within *Lobatopteris*, but recognize that it (perhaps together with *Pecopteris lobulata* Dalinval and certain other Westphalian pecopteroid species) may eventually be transferred to another, possibly new, form-genus for larger, more divided fronds producing trilete spores.

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